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A reappraisal of *Theroteinus* (Haramiyida, Mammaliaformes) from the upper triassic of Saint-Nicolas-de-Port (France)

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Abstract

The earliest mammaliaforms are difficult to ~~describe~~ because the fossil record is poor and because their distinctive morphologies cannot be directly compared with more recent mammaliaforms. This is especially true for the haramiyid genus *Theroteinus*, only known in the Saint-Nicolas-de-Port locality (Rhaetian, France). This study presents a new definition of the type-species *Theroteinus nikolai*. A new species *Theroteinus rosieriensis*, sp. nov., is distinguished by the lingual shift of distal cusps, a larger size, and a more stocky occlusal outline. Comparisons with *Eleutherodon*, *Megaconus* and *Millsodon* suggest that *Theroteinus* has potential close relatives among the Jurassic haramiyids.

Introduction

The earliest mammaliaforms are notoriously poorly known because of the scarcity of specimens (most often isolated teeth) and the difficulty to assess their relationships with later mammaliaforms (including mammals themselves). Among them, haramiyids have long been considered as a very peculiar ~~and~~ difficult to study ~~group~~ (*e.g.*, Simpson, 1928; Kielan-Jaworowska, Cifelli & Luo, 2004). However, even within haramiyids, the genus *Theroteinus* Sigogneau-Russell, Frank & Hemmerlé, 1986 is distinctive and always set apart. This genus was hitherto known only by a dozen of isolated teeth, all from the locality of Saint-Nicolas-de-Port (Rhaetian, north eastern France), which has yielded a very diversified and abundant micro-vertebrate assemblage (see below). Because of the distinctive morphology of *Theroteinus*, some authors cast doubt on its haramiyidan referral (Sigogneau-Russell, 1983a; Sigogneau-Russell, Frank & Hemmerlé, 1986) and later placed it away from all other haramiyids (Hahn, Sigogneau-Russell & Wouters, 1989; Butler, 2000; Hahn & Hahn, 2006). Recently, several new haramiyids were described which significantly increased the diversity of the order (*e.g.*, Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014). In this study, new *Theroteinus* material is described and gives support for a systematic reassessment and an update of relationships of this genus within haramiyids.

Historical background

In 1983, Sigogneau-Russell described three very particular teeth: MNHN.F.SNP 61 W was considered to represent a new haramiyid and MNHN.F.SNP 78 W, and MNHN.F.SNP 2 Ma were considered to represent a multituberculate (Sigogneau-Russell, 1983a). Three years later, the new genus and new species *Theroteinus nikolai* Sigogneau-Russell, Frank & Hemmerlé, 1986 was erected and included in its monotypic family Theroteinidae Sigogneau-Russell, Frank & Hemmerlé, 1986. Sigogneau-Russell, Frank & Hemmerlé (1986) included MNHN.F.SNP 78 W, and MNHN.F.SNP 2 Ma, considered as upper teeth, in the hypodgim of the species *T. nikolai*, in association with one upper tooth and three lower teeth, which were then not described. They studied the enamel ultrastructure and the micro-wear of these teeth and interpreted the absence of wear striation as indicating an essentially vertical masticatory movement (Sigogneau-Russell, Frank & Hemmerlé, 1986). Hahn, Sigogneau-Russell & Wouters (1989) described four new specimens (two upper and two lower teeth) and established *Theroteinus* sp. based on four

lower teeth characterized by their small size, including MNHN.F.SNP 61 W along with MNHN.F.SNP 226, MNHN.F.SNP 366, and MNHN.F.SNP 497 W.

Hahn, Sigogneau-Russell & Wouters (1989) included *Theroteinus*, other haramiyids, and Multituberculata Cope, 1884 within Allotheria Marsh, 1880. They erected the order Theroteinida Hahn, Sigogneau-Russell & Wouters, 1989 beside the sub-order Haramiyoidea Hahn, 1973, which they raised to ~~the~~ ordinal rank as Haramiyida Hahn, Sigogneau-Russell & Wouters, 1989. Their classification was illustrated by a phylogenetic tree in which *Theroteinus* is the sister-group of all other allothers (Hahn, Sigogneau-Russell & Wouters, 1989: Text-fig. 12). Butler (2000) modified the classification of Allotheria. Within the order Haramiyida of Hahn, Sigogneau-Russell & Wouters (1989), he ~~described two sub-orders:~~ Theroteinida ~~of~~ Hahn, Sigogneau-Russell & Wouters (1989) and Haramiyoidea ~~of~~ Hahn (1973) (Butler, 2000). Hahn & Hahn (2006) published the ~~last~~ most recent classification of Haramiyida including *Theroteinus*. They changed the names of the sub-orders of Butler (2000) respectively in Theroteinina and Haramiyina and included *Millsodon* Butler & Hooker, 2005 (Middle Jurassic, England) into the family Theroteinidae (Hahn & Hahn, 2006).

In all of these classifications, *Theroteinus* is always considered as more primitive than other haramiyids upon one main feature: in centric occlusion, one tooth ~~of *Theroteinus*~~ is in contact with two opposite teeth ('one-to-two' occlusion). This feature is shared by other mammaliaforms such as morganucodonts and kuehneotheriids but not by other haramiyids, which are characterized by one tooth is in contact with only one ~~opposite~~ tooth in centric occlusion ('one-to-one' occlusion).

Geology and associated fauna

The ancient sand quarry of Saint-Nicolas-de-Port, a locality close to the city of Nancy in eastern France, has yielded an abundant collection of vertebrate microremains (Sigogneau-Russell & Hahn 1994). The site is part of the sandy succession of the ‘Grès infraliasiques’ Formation, considered as deposits in a shallow marine platform (Debuysschere, Gheerbrant & Allain, 2015 and references therein). The vertebrate collections from Saint-Nicolas-de-Port display an important diversity of species belonging to Chondrichthyes, Dipnoi, Actinopterygia, Temnospondyli, Sauropsida, non-mammalian Cynodontia, and Mammaliaformes (Debuysschere,

Gheerbrant & Allain, 2015 and references therein). Saint-Nicolas-de-Port yields especially the most abundant and most diverse Upper Triassic assemblage of mammals (Sigogneau-Russell & Hahn, 1994; Kielan-Jaworowska, Cifelli & Luo, 2004; Debuysschere, Gheerbrant & Allain, 2015), including morganucodonts (Debuysschere, Gheerbrant & Allain, 2015), kuehneotheriids (Debuysschere, 2016), haramiyids (Sigogneau-Russell, 1989; 1990), woutersiids (Sigogneau-Russell, 1983b; Sigogneau-Russell & Hahn, 1995), the problematic *Delsatia* Sigogneau-Russell & Godefroit, 1997, and theroteinids that are reviewed here.

Institutional and other abbreviations

BDUC: Biology Department, University College, London, United Kingdom;
MNHN: Muséum National d'Histoire Naturelle, Paris, France;
RAS: Rosières-aux-Salines, another name for the study site;
RBINS: Royal Belgian Institute of Natural Sciences, Bruxelles, Belgium;
SNP: Saint-Nicolas-de-Port.

Material

This study describes 20 isolated teeth of haramiyids from Saint-Nicolas-de-Port. Denise Sigogneau-Russell and her co-workers have excavated only one stratigraphical level in the sand ~~quarry~~. Specimens collected at this time are kept both in the MNHN, with the acronym 'SNP', and in the RBINS, with the acronym 'RAS'. Several amateur palaeontologists gathered their own collections alongside Sigogneau-Russell's team and donated them to MNHN and RBINS. The collection of Georges Wouters is identified by the suffix 'W' or 'FW', and the collection of M. Marignac is identified by the suffix 'Ma'. However, there are no data on the exact, original stratigaphic level within the quarry of these collections. All the specimens described by Sigogneau-Russell, Frank & Hemmerlé (1986), and Hahn, Sigogneau-Russell & Wouters (1989) are considered here, alongside with eight new specimens (MNHN.F.SNP 14 FW, MNHN.F.SNP 787, RBINS RAS 3 FW, RBINS RAS 11 FW, RBINS RAS 62 FW, RBINS RAS 74 FW, RBINS RAS 77 FW, RBINS RAS 103 FW).

Methods

121

122 **Observations, drawings and measurements**

123 All specimens were observed with a binocular microscope (CETI, Medline Scientific, Chalgrove,
124 United Kingdom) at a magnification power of 36. A camera lucida mounted on the microscope
125 was used for drawings. Measurements were taken with a digital readout for metrology
126 (Heidenhain ND 1200, Traunreut, Germany). These measurements were used to make diagrams
127 and statistical tests with Excel (Microsoft, Redmond, Washington, 2013) and statistical tests with
128 the R statistical environment (R development Core Team, 2016). The 3D images of studied teeth
129 were obtained by X-ray Computed Tomographic (CT) scans at the AST-RX platform of the
130 MNHN using a phoenix|x-ray|v|tome|x L 240-180 CT scanner (GE Measurement & Control
131 Solutions, Billerica, Massachusetts) (Table S1). The 3D data were processed with Materialise
132 Mimics Innovation Suite 17.0 Research Edition (Materialise NV, Leuven, Belgium, 2014). The
133 SEM photos were obtained by scanning electron microscope at the RBINS using a FEI
134 QUANTA 200 ESEM (FEI, Hillsboro, Oregon) with a voltage of 15 kV and a dwell of 10 µs.

135

136 **Dental nomenclature**

137 The nomenclature used here to describe the haramiyid teeth is derived from Parrington (1947:
138 Fig. 3), Hahn (1973: p. 5), Butler & MacIntyre (1994: p. 435), and Butler (2000: p. 319). The
139 row of cusps named *a* is characterized by less numerous, and well-individualized cusps. The
140 second row of cusps is named *b*. Both rows define a central basin. Additional cusps are named
141 *aa* when they are on the flank of the row *a*, and *bb* when they are on the flank of the row *b*. In
142 each row, cusps are numbered starting from number 1. On lower teeth, the numbering starts from
143 the mesial extremity, while on upper teeth, it starts from the distal extremity. The term ‘u-ridge’
144 refers to the junction of crests which close the basin at its distal extremity on lower teeth and its
145 mesial extremity on upper teeth. The term ‘saddle’ refers to the junction of two crests which
146 delimits the basin at its open extremity, respectively mesial on lower teeth and distal on upper
147 teeth. This nomenclature is used only in a descriptive ~~purpose~~. The homonymy does not
148 necessarily imply homology. Capital letters are used for upper teeth and lower case letters for
149 lower teeth.
150 The descriptions of the wear facets are based on the nomenclature of Koenigswald et al. (2013:
151 p. 146) for jaw movements. This nomenclature is used to define the direction and the angle of the

slope of the wear facets. The process and the pattern of the occlusion are beyond the scope of this article and will be dealt with in detail later on.

Methodology of characterization of Saint-Nicolas-de-Port material

The haramiyid teeth are distinguished from other contemporary mammaliaforms by the presence of longitudinal rows of cusps separated by basins. The material referred to *Theroteinus* is distinguished from material referred to *Thomasia* Poche, 1908 by their low cusps in relation to their diameter and a basin smaller in length and width. All specimens described here are considered to be molariforms, owing to their resemblance with molariforms of other haramiyids (*e.g.*, Butler, 2000) and the absence of characters that could be related to the position in the dental series (see below).

The lower molariforms are distinguished from the upper molariforms by the presence of, respectively, two or three rows of cusps and by the form of ~~the~~ row *a*/*A*. In lower molariforms, the lingual row *a* includes the largest cusps. ~~The c~~usp *a1* is especially much larger than the others cusps and it is located on the mesiolingual side of the crown. In upper molariforms, the labial row *A* shows three sub equal cusps, when the central row *B* shows a cusp *B2* larger than the other cusps of the row and located on the distal side of the crown.

Nomenclatural acts

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:57401966-D5B5-468C-94FD-115C0C32FE00. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Systematic

183
184 **Mammaliaformes** Rowe, 1988
185 Order **Haramiyida** Hahn, Sigogneau-Russell & Wouters, 1989
186 Sub-order **Theroteinida** Hahn, Sigogneau-Russell & Wouters, 1989
187
188 **Synonymy.** Theroteinina Hahn & Hahn, 2006: p. 189.
189
190 **Type-family.** Theroteinidae Sigogneau-Russell, Frank & Hemmerlé, 1986, by monotypy.
191
192 **Emended diagnosis.** As for the type-family.
193
194 **Distribution.** As for the type-family.
195
196 Family **Theroteinidae** Sigogneau-Russell, Frank & Hemmerlé, 1986
197
198 **Type-genus.** *Theroteinus* Sigogneau-Russell, Frank & Hemmerlé, 1986.
199
200 **Emended diagnosis.** As for the type-genus.
201
202 **Distribution.** As for the type-genus.
203
204 Genus ***Theroteinus*** Sigogneau-Russell, Frank & Hemmerlé, 1986
205
206 **Type-species.** *Theroteinus nikolai* Sigogneau-Russell, Frank & Hemmerlé, 1986.
207
208 **Referred species.** *Theroteinus rosieriensis* sp. nov.
209
210 **Emended diagnosis.** Haramiyids with lower and upper molariforms showing low cusps with
211 more extended base and more massive aspect, short and narrow basins in relation to the size of
212 crown, presence of only two cusps in row *a* on lower molariforms (shared with some specimens

of *Thomasia*), presence of a row *BB* on upper molariforms (potentially shared with *Eleutherodon*, *Megaconus* and *Millsodon*), and an essentially vertical, masticatory movement.

Distribution. Upper Triassic (Rhaetian): France, Lorraine, Saint-Nicolas-de-Port ("Grès infraliasiques" Formation).

Theroteinus nikolai Sigogneau-Russell, Frank & Hemmerlé, 1986

Figs. 1-3

Synonymy. *Theroteinus* sp. Hahn, Sigogneau-Russell & Wouters, 1989: p. 210.

Emended diagnosis. *Theroteinus nikolai* differs from *T. rosieriensis* by smaller molariforms (Tables 1-3, Fig. 7A), a larger length/width ratio (Tables 1-3, Fig. 7B), a cusp *B2* more labial than the lingual basin (Figs. 1A, 3A), and a cusp *b4* more labial than the saddle (Figs. 2, 3B-E).

Holotype. MNHN.F.SNP 78 W (Figs. 1A, 3A), right upper molariform, from Saint-Nicolas-de-Port (Upper Triassic, France).

Referred material.

Lower molariforms. MNHN.F.SNP 61 W (right) (Figs. 2A, 3B), MNHN.F.SNP 226 W (left) (Fig. 1C), MNHN.F.SNP 366 W (right) (Figs. 2B, 3C), MNHN.F.SNP 497 W (right) (Figs. 2C, 3D), MNHN.F.SNP 787 (right) (Fig. 3E).

Upper molariforms. MNHN.F.SNP 722 (right) (Fig. 1B), RBINS RAS 103 FW (right)

Measurements. See Table 1.

Description.

Lower molariforms. The crown is dominated by two longitudinal rows of cusps which delimit a central basin, the lingual row *a* and the labial row *b*. The central basin is delimited mesially by the saddle which joins ~~the~~ cusps *a1* and *b2*, and distally by the u-ridge which joins

~~the~~ rows *a* and *b*. The central basin gets deeper and narrower from the mesial extremity to the distal extremity.

~~The row~~ *a* includes two cusps. ~~The cusp~~ *a1* is the largest cusp of the tooth and rises vertically in lateral view. This cusp extends over the mesial half of the tooth. ~~The cusp~~ *a1* shows a mesial weak carina which splits into two segments. One segment goes mesially and the other bents labially to join the cusp *b1*. At the level of the base of cusp *b1*, the mesial segment turns into a short, horizontal cingulum to join ~~the~~ cusp *b1*. A distal crest starts from the distolabial side of the apex of cusp *a1* to join the cusp *a2*. This crest is straight in lateral view, but it is curved labially in occlusal view. A sulcus underlines the lingual side of this crest and descends to the base of cusp *a1*. A second crest, straight in occlusal and lateral views, starts from the labial side of the apex of cusp *a1* to the base, where it takes part in the saddle. The distal and labial crests delimit a concave, narrow surface on the distolabial flank of cusp *a1*, which extends from the apex to the central basin. ~~The cusp~~ *a2* is twice lower and labiolingually narrower, and much mesiodistally shorter than cusp *a1*. ~~The cusp~~ *a2* is more lingual than cusp *a1*. The lingual flanks of cusps *a1* and *a2* are aligned and parallel to the mesiodistal axis of the tooth on MNHN.F.SNP 61 W, but deviate distolabialy on MNHN.F.SNP 366 W, and MNHN.F.SNP 787. The occlusal outline of cusp *a2* is semi-circular with a convex, lingual side and nearly flat, labial side. The labial side shows a vertical, weak ridge in the middle. In distal view, the slope of the labial flank is more vertical than the slope of the lingual flank. The latter is slightly convex. In labial view, the mesial base of cusp *a2* is higher than the distal base of the cusp. In lingual view, the bases of cusps *a1* and *a2* are at the same level. ~~The cusp~~ *a2* shows two crests, respectively mesial and distal, straight in lateral and occlusal views, and aligned mesiodistally. The first crest starts from the mesiolabial side of the apex to join the distolingual crest of cusp *a1*. The second crest starts from the distolabial side of the apex to the extremity of ~~the~~ row *a*. The distal crest is much longer than the mesial crest. The slope of the mesial crest of cusp *a2* is weaker than the slope of the distal crest of cusp *a1* and the slope of the distal crest of cusp *a2*, the slope of the latter is more vertical than the slope of distal crest of cusp *a1*.

~~The row~~ *b* includes four cusps, less distinguished from each other than cusps of row *a*. ~~The cusp~~ *b1* is the most mesial of the tooth. This cusp is sub-equal in size with cusp *b4*, or larger in MNHN.F.SNP 61 W. ~~The cusp~~ *b1* is located in front of the saddle, but tends to rise lingually to join the mesiolabial carina of cusp *a1*. ~~The cusp~~ *b2* is the largest cusps of row *b*. This cusp is

slightly smaller than cusp *a1*, except in MNHN.F.SNP 366 W where cusp *b2* is slightly larger and higher than cusp *a1*. ~~The cusp~~ *b2* is labial to cusp *a1*, its base extends as mesially but much less distally, and its apex is slightly more distal, or much more distal in MNHN.F.SNP 61 W. ~~The cusp~~ *b2* shows two crests, straight in occlusal and lateral views. The first crest ~~goes~~ labially, but mesiolabially in MNHN.F.SNP 61 W, to take part in the saddle. The second crest ~~goes~~ distally and join cusp *b3*. Both crests define on the one side a slightly convex, distolingual occlusal outline, and on the other side a large arc of a circle. ~~The cusp~~ *b3* is much smaller than cusps *a1*, *a2*, and *b2* and slightly smaller than cusps *b1* and *b4*. ~~The cusp~~ *b3* is directly distal to cusp *b2*, except in MNHN.F.SNP 787 where it is slightly more labial. This cusp is more mesial than *a1-a2* notch in MNHN.F.SNP 787, aligned with *a1-a2* notch in MNHN.F.SNP 366 W, and more distal than *a1-a2* notch in MNHN.F.SNP 61 W. The apex of cusp *b3* is slightly higher than the apex of cusp *a2*, or at the same level in MNHN.F.SNP 61 W. The long axis of cusp *b3* slightly deviates distolingually from the mesiodistal axis of the tooth, except in MNHN.F.SNP 787 where both axes are parallel. ~~The cusp~~ *b4* is distal to cusp *b3* and slightly more lingual. Consequently, the long axes of both cusps are aligned, except in MNHN.F.SNP 787. The apex of cusp *b4* is situated slightly lower than the apex of cusp *a2* and faces the distal crest of cusp *a2*. The cusp *b4* shows a lingual carina, which is well developed in MNHN.F.SNP 787. The u-ridge is a low crest which extends row *b* and bends lingually to join the extremity of row *a*.

Comments on MNHN.F.SNP 266 W and MNHN.F.SNP 497 W. MNHN.F.SNP 266 W and MNHN.F.SNP 497 W are difficult to describe because ~~their morphology is~~ damaged. The surface of MNHN.F.SNP 266 W is not well preserved (Fig. 1C) and MNHN.F.SNP 497 W is heavily worn. As consequence, the cusps are difficult to ~~be~~ describe~~d~~. For these reasons, they ~~are~~ not been incorporated in the description above. About MNHN.F.SNP 497 W, it may be noticed that row *b* is less developed than in other specimens, with a strong reduction of cusp *b4* (Figs. 2C, 3D). In the absence of clear morphological characters, both specimens are referred to *Theroteinus nikolai* following morphometry (see Comparisons. Characterisation of *Theroteinus* species below).

Upper molariforms. The crown is dominated by three longitudinal rows of cusps: labial row *A*, central row *B* and lingual row *BB*. ~~The rows~~ *A* and *B* define a labial basin delimited distally by

the saddle, constituted only by the lingual crest of cusp *A2*, and mesially by the u-ridge which joins rows *A* and *B*. The rows *B* and *BB* define a lingual basin, smaller than the labial basin, delimited distally by the meeting of cusps *B2* and *BB1*, and mesially by the crest which joins rows *B* and *BB*. Both basins get deeper and larger mesially.

~~The row~~ *A* includes three mesiodistally aligned cusps. The three cusps are situated at the same level on the crown. ~~The cusps~~ *A1* and *A3* are sub-equal in length and width, cusp~~s~~ *A1* is slightly higher than cusp *A3*. ~~The cusp~~ *A2* is twice times mesiodistally longer and higher, and ~~much more~~ labiolingually wider than cusps *A1* and *A3*. The occlusal outlines of cusps *A1* and *A3* show a semi-circular, labial flank and a relatively flat, lingual flank, sometimes concave because of wear. ~~The cusp~~ *A1* shows two crests, straight in occlusal and lateral views. The longest crest ~~goes~~ distolingually from the apex to cusp *B1*. The other crest ~~goes~~ mesially to cusp *A2*. The slopes of these crests are sub-equal. The cusp *A3* shows two crests, straight in occlusal and lateral views. The longest crest goes mesiolingually from the apex to take part in the u-ridge. The other crest goes distally to cusp *A2*. The slopes of these crests are sub-equal. The cusp *A2* shows three crests, straight in occlusal and lateral views. The first crest goes distally to cusp *A1*. The second crest goes mesially to cusp *A3*. The third crest goes lingually but does not join another structure. The distal crest is the shortest and shows the strongest slope. The lingual crest is much wider than both other crests. The lingual and mesial crests define a flat surface on the mesiolingual flank of cusp *A2*. The *A1-A2* and *A2-A3* notches are equal in depth, but *A1-A2* notch is situated higher than *A2-A3* notch.

A small, supplementary cusp is situated under the labial flank of cusp *A3*.

The row *B* includes five cusps. The cusp *B1* looks like a distally curved semi-circle. This cusp~~s~~ is slightly smaller in length and width than cusp *A1*, but much ~~smaller in high~~. The cusp *B1* is more distal and more lingual than cusp *A1* and is mesiodistally aligned with the saddle. ~~The cusp~~ *B2* is slightly smaller than cusp *A2*. ~~The cusp~~ *B2* is much more lingual than cusp *B1* and is labiolingually aligned with *A1-A2* notch. This cusp is cone-shaped and does not show any crest. Three small cuspules are situated at the base of the mesiolingual flank of cusp *B2*. ~~The cusp~~ *B3* is directly mesial to cusp *B2*. The apex of cusp *B3* is slightly more labial the apex of cusp *B2* and slightly more mesial than apex of cusp *A2*. ~~The cusp~~ *B3* is sub-equal in size with cusp *B1* and is situated slightly lower than cusp *B2*. ~~The cusp~~ *B4* is directly mesial to cusp *B3*. This cusp is smaller in all dimension and situated lower than cusp *B3*. ~~The cusp~~ *B4* is labiolingually aligned

with *A2-A3* notch. The cusp *B5* is the most mesial cusp of the tooth. This cusp is smaller in all dimension, situated lower, and slightly more labial than cusp *B4*. The mesial extremity of cusp *B5* show tow crests. One crest goes labially to take part in the u-ridge of labial basin. The other crest goes lingually to mesially close the lingual basin.

The row *BB* includes two cusps. The cusp *BB1* is sub-equal in size to cusp *B4* and is situated at the same level. The cusp *BB1* is placed right next to cusps *B2* and *B3*, directly lingual to *B2-B3* notch. The cusp *BB2* is mesial to cusp *BB1* but slightly more lingual. This cusp is sub-equal in length and width with cusp *B5*, but slightly higher. A cusp *BB3* was possibly present, but this part of the crown is broken. The row *BB* is extended by a crest which goes mesially and next bends labially to close the lingual basin.

Comments on MNHN.F.SNP 722. Only the distal part of MNHN.F.SNP 722 is preserved, with cusps *A1*, *B1*, *B2*, *BB1*, and a part of cusps *A2* and *B3* (Fig. 1B). Since morphometry is not applicable, this specimen is referred to *Theroteinus nikolai* following the position of cusp *B2* in relation to cusps *B3* and *BB1*. However, some doubts remain because cusp *B3* is fragmentary. MNHN.F.SNP 722 differs from MNHN.F.SNP 78 W by a smaller cusp *A1* and presence of only one cuspule at the base of mesiolingual flank of cusp *B2*.

Wear.

Lower molariforms. In MNHN.F.SNP 787, only the apices of cusps are abraded by wear. In MNHN.F.SNP 366 W, the apices of cusps *a1* and *a2* shows a shallow, distal facet. The apex of cusp *b1* shows a steep, mesiolabial facet. The apex of cusp *b2* shows a shallow, distal facet. The cusp *b3* shows a steep, labial facet, which slightly extends on the mesial part of cusp *b4*. The cusp *b4* shows a shallow, distal facet. The sides of basin shows traces of wear but do not develop clear facet. In MNHN.F.SNP 61 W, the facets on apices of cusps *a1* and *b2* are more extended labially and the carina of cusp *a1* is flattened. MNHN.F.SNP 61 W differs from MNHN.F.SNP 366 W by a horizontal facet on cusp *b3*. In MNHN.F.SNP 497 W, the distal parts of cusps *a1* and *a2* each show a shallow, distal facet. The distal part of cusps *b2*, *b3*, and *b4* shows one shallow, distal facet. The rest of cusps *a1* and *b2*, and cusp *b1* are abraded by wear.

366 **Upper molariforms.** In MNHN.F.SNP 722, only the apices of cusps are abraded by wear.
367 MNHN.F.SNP 78 W shows a large number of well-defined facets. The apex of cusp *A1* shows a
368 steep, distolingual facet. The apex of cusp *A2* shows a horizontal, mesial facet. This facet is
369 connected with traces of wear on the mesiolingual side of the cusp which spread from the apex to
370 the labial basin. The lingual crest of cusp *A2* is slightly flattened by wear. The lingual side of
371 cusp *A3* is truncated by a concave, steep, lingual facet. Cusp *B1* shows diffuse traces of wear but
372 no distinct wear facet. The apex of cusp *B2* shows a horizontal, mesial facet. The mesiolingual
373 and labial sides of cusp *B2* show~~s~~ slight traces of wear. The apex of cusp *B3* shows a shallow,
374 mesio-mesiolingal facet. The apex of cusp *B4* shows a steep, mesio-mesiolingual facet. ~~The cusp~~
375 *B5* shows a concave, shallow, lingual facet. The apex of cusp *BB1* seems to show a horizontal
376 facet but is partially broken. ~~The cusp~~ *BB2* shows a steep, mesial facet. The flanks of the labial
377 basin show~~s~~ traces of wear.
378
379 ***Theroteinus rosieriensis*** sp. nov.
380 urn:lsid:zoobank.org:act:F3C6B3B3-1733-4625-942F-9C085A51116A
381 Figs. 4-6
382
383 **Etymology.** rosieri-: a Latinized form of ‘Rosières’ from ‘Rosières-aux-salines‘, another name
384 used for the study site; -ensis; suffix added to a toponym to form an adjective.
385
386 **Diagnosis.** *Theroteinus rosieriensis* differs from *T. nikolai* by larger molariforms (Tables 1-3,
387 Fig. 7A), a ~~smaller~~ length/width ratio (Tables 1-3, Fig. 7B), a cusp *B2* mesiodistally aligned with
388 the lingual basin (Figs. 1A, 3A), and a cusp *b4* mesiodistally aligned with the saddle (Figs. 2,
389 3.B-E).
390
391 **Holotype.** MNHN.F.SNP 2 Ma (Figs. 4A, 6A), right upper molariform, ~~from~~ Saint-Nicolas-de-
392 Port (Upper Triassic, France).
393
394 **Referred material.**
395 **Lower molariforms.** MNHN.F.SNP 309 W (left) (Figs. 4B, 6C), MNHN.F.SNP 487 W (left)
396 (Figs. 4C, 6D), RBINS.RAS 3 FW (right), RBINS.RAS 11 FW (left), RBINS.RAS 62 FW

(right) (Fig. 5A), RBINS.RAS 74 FW (right) (Fig. 5B), RBINS 77 FW (right) (Fig. 5C), RBINS.RAS 800 (right)

Upper molariforms. MNHN.F.SNP 14 FW (right), MNHN.F.SNP 335 W (right) (Fig. 6B), RBINS.RAS 801 (left)

Measurements. See Table 1.

Description.

Lower molariforms. The crown is dominated by two longitudinal rows of cusps which delimit a central basin, the lingual row *a* and the labial row *b*. The central basin is delimited mesially by the saddle which joins ~~the~~ cusps *a1* and *b2* and distally by the u-ridge which joins ~~the~~ rows *a* and *b*. The saddle is very high compared with the u-ridge, except in MNHN.F.SNP 309 W where the difference is weaker. The central basin gets deeper and narrower from the mesial extremity to the distal extremity.

~~The row~~ *a* includes two cusps. ~~The cusp~~ *a1* is the largest cusp of the tooth and rises vertically in lateral view. This cusp extends over the mesial half of the tooth, even more in MNHN.F.SNP 487 W, RBINS.RAS 74 FW, and RBINS.RAS 77FW. ~~The cusp~~ *a1* shows a mesial weak carina which splits into two segments. One segment ~~goes~~ mesially and the other bents labially to join ~~the~~ cusp *b1*. At the level of the base of cusp *b1*, the mesial segment turns into a short, horizontal cingulum to join ~~the~~ cusp *b1*. A distal crest starts from the distolabial side of the apex of cusp *a1* to join the cusp *a2*. This crest is straight in lateral view, but it is curved labially in occlusal view, except in MNHN.F.SNP 487 W, RBINS.RAS 62 FW, and RBINS.RAS 74 FW where it is straight in both views. A sulcus underlines the lingual side of this crest and descends to the base of cusp *a1*, absent in MNHN.F.SNP 487 W and RBINS.RAS 74 FW. A second crest, straight in occlusal and lateral views, starts from the labial side of the apex of cusp *a1* to the base, where it takes part in the saddle. The distal and labial crests delimit a concave, narrow surface on the distolabial flank of cusp *a1*, which extends from the apex to the central basin. ~~The cusp~~ *a2* is half as high, labiolingually wide, and mesiodistally long as cusp *a1*, even less in RBINS.RAS 74 FW. The cusp *a2* is more lingual than cusp *a1*. The lingual flanks of cusps *a1* and *a2* are aligned and deviate ~~distolabially~~ from the mesiodistal axis of the tooth. The occlusal outline of cusp *a2* is semi-circular with a convex, lingual side and nearly flat, labial side, except in MNHN.F.SNP 487

W because of wear. In distal view, the slopes of the labial and lingual flanks are sub-equal. The latter is slightly convex. In labial view, the mesial base of cusp *a2* is higher than the distal base of the cusp. In lingual view, the bases of cusps *a1* and *a2* are at the same level. ~~The cusp~~ *a2* shows two crests, respectively mesial and distal, straight in lateral and occlusal views, and aligned mesiodistally. The first crest starts from the mesiolabial side of the apex to join the distolingual crest of cusp *a1*. The second crest starts from the distolabial side of the apex to the extremity of ~~the~~ row *a*. The distal crest is much longer than the mesial crest. The slope of the mesial crest of cusp *a2* is weaker than the slope of the distal crest of cusp *a1* and the slope of the distal crest of cusp *a2*, the slope of the latter is more vertical than the slope of distal crest of cusp *a1*. These crests are not preserved in MNHN.F.SNP 487 W and RBINS.RAS 74 FW.

~~The row~~ *b* includes four cusps, less distinguished from each other than cusps of row *a*. ~~The cusp~~ *b1* is the most mesial of the tooth. This cusp is sub-equal in high and mesiodistal length with cusp *a2* but wider and more voluminous. ~~The cusp~~ *b1* is located in front of the saddle, but tends to rise lingually to join the mesiolabial carina of cusp *a1*. ~~The cusp~~ *b2* is the largest cusps of row *b*. This cusp is slightly smaller than cusp *a1*, except in MNHN.F.SNP 309 W and RBINS.RAS 62 FW where it is very smaller but still larger than other cusps. The cusp *b2* is labial to cusp *a1*, its base extends less mesially and distally, and its apex is slightly more distal, or much more distal in MNHN.F.SNP 309 W. ~~The cusp~~ *b2* shows two crests, straight in occlusal and lateral views. The first crest ~~goes~~ labially to take part in the saddle. The second crest ~~goes~~ distally and joins cusp *b3*. Both crests define on the one side a slightly convex, distolingual occlusal outline, and on the other side a large arc of a circle. This part of the crown has been ~~damaged~~ by wear in MNHN.F.SNP 487 W. ~~The cusp~~ *b3* is much smaller than cusps *a1*, *a2*, *b1*, and *b2* and slightly smaller than cusp *b4*. The cusp *b3* is distal and slightly lingual to cusp *b2*. This cusp is labiolingually aligned with *a1-a2* notch. The base of cusp *b3* is slightly lower than the base of cusp *a2*. The long axis of cusp *b3* slightly distolingually ~~deviates~~ from the mesiodistal axis of the tooth. This part of the crown is ~~damaged~~ by wear in RBINS.RAS 74 FW and RBINS.RAS 77 FW. The cusp *b4* is distal to cusp *b3* and slightly more lingual. ~~The cusp~~ *b4* is mesiodistally aligned with the saddle and labiolingually aligned with the distal crest of cusp *a2*. The base of cusp *b4* is slightly lower than the base of cusp *b3*. In MNHN.F.SNP 487W, RBINS.RAS 62 FW, and RBINS.RAS 77 FW, a low crest extends ~~the~~ row *b* and bends ~~lingual~~ to join the extremity of row *a*. In MNHN.F.SNP 309 W and RBINS.RAS 74 FW, this crest splits into two segments. The

first segment bends lingually to join the extremity of row *a*. The second segment bends labially and ~~goes~~ down the side of the crown and turns into a thin bulge which extends into the base of cusp *b2*.

Comments on RBINS.RAS 800. The occlusal surface of RBINS.RAS 800 is not well preserved. As consequence, the cusps are difficult to ~~be~~ described. For these reasons, this specimen ~~is~~ not been included in the description above. In the absence of clear morphological characters, this specimen is referred to *Theroteinus rosieriensis* following morphometry (see Comparisons. Characterisation of *Theroteinus* species below).

Upper molariforms. The crown is dominated by three longitudinal rows of cusps: labial row *A*, central row *B* and lingual row *BB*. ~~The rows~~ *A* and *B* define a labial basin delimited distally by the saddle, constituted only by the lingual crest of cusp *A2*, and mesially by the u-ridge which joins rows *A* and *B*. ~~The rows~~ *B* and *BB* define a lingual basin, smaller than the labial basin, delimited distally by the meeting of cusps *B2* and *BB1*, and mesially by the crest which joins rows *B* and *BB*. Both basins get deeper and larger mesially. The lingual basin is very shallow in MNHN.F.SNP 335 W.

~~The row~~ *A* includes three cusps. In MNHN.F.SNP 335 W, cusp *A3* is slightly more labial than cusps *A1* and *A2*. In MNHN.F.SNP 2 Ma, cusp *A1* is more lingual than cusp *A2* and cusp *A3* is more labial than cusp *A2*. The three cusps are located at the same level on the crown. ~~The cusps~~ *A1* and *A3* are sub-equal in height and width, cusp~~s~~ *A1* is slightly longer than cusp *A3*. ~~The cusp~~ *A2* is twice times mesiodistally longer and higher, and much labiolingually wider than cusps *A1* and *A3*. In MNHN.F.SNP 2 Ma, cusps *A1* and *A3* are less wide compared with cusp *A2*. In occlusal view, ~~the cusps~~ *A1* and *A3* show a semi-circular labial flank and a relatively flat, lingual flank. ~~The cusp~~ *A1* shows two crests, straight in occlusal and lateral views. The longest crest ~~goes~~ distolingually from the apex to cusp *B1*. The other crest ~~goes~~ mesially to cusp *A2*. In MNHN.F.SNP 2 Ma, the mesial crest is present but cusp *A1* shows a flat side in front of cusp *B1*. ~~The cusp~~ *A3* shows two crests, straight in occlusal and lateral views. The longest crest ~~goes~~ mesiolingually from the apex to take part in the u-ridge. The other crest ~~goes~~ distally to cusp *A2*. The slope of the distal crest is more vertical than the slope of the mesial crest. ~~The cusp~~ *A2* shows three crests, straight in occlusal and lateral views. The first crest ~~goes~~ distally to cusp *A1*.

The second crest ~~goes~~ mesially to cusp *A3*. The third crest ~~goes~~ lingually but does not join another structure. The distal crest is the shortest. ~~The~~ slopes of three crests are sub-equal. The lingual crest is much wider than both other crests. The lingual and mesial crests define a concave surface on the mesiolingual flank of cusp *A2*. The *A1-A2* notch is less ~~depth~~ and is situated higher than *A2-A3* notch.

~~The row~~ *B* includes four cusps. ~~The cusp~~ *B1* is sub-equal in size with cusp *A1* in MNHN.F.SNP 2 Ma, but smaller in MNHN.F.SNP 335 W. ~~The cusp~~ *B1* is more distal and more lingual than cusp *A1* and is mesiodistally aligned with the saddle. ~~The cusp~~ *B2* is slightly smaller than cusp *A2*. ~~The cusp~~ *B2* is much more lingual than cusp *B1* and is labiolingually aligned with *A1-A2* notch. This cusp is cone-shaped and does not show any crest. One small cuspule is situated at the base of the mesiolingual flank of cusp *B2*. The *B2-B3* notch is labiolingually aligned with cusp *A2*. ~~The cusp~~ *B3* is more labial than cusp *B2* and slightly more lingual than cusp *B1* (MNHN.F.SNP 2 Ma) or mesiodistally aligned with cusp *B1* (MNHN.F.SNP 335 W). ~~The cusp~~ *B3* is much smaller than cusps *A2* and *B2* and slightly larger than cusps *A1*, *A3*, and *B1* (MNHN.F.SNP 2 Ma) or sub-equal ~~with~~ cusps *A1* and *A3* (MNHN.F.SNP 335 W). In MNHN.F.SNP 2 Ma, cusp *B3* is wider than long. ~~The cusp~~ *B3* is situated slightly lower than cusp *B2*. The *B3-B4* notch is labiolingually aligned with *A2-A3* notch. ~~The cusp~~ *B4* is directly mesial to cusp *B3*. This cusp is smaller in all dimensions and located lower than cusp *B3*. In MNHN.F.SNP 335 W, a cusp *B5* was potentially present but removed by wear. The mesial extremity of row *B* shows two crests. One crest ~~goes~~ labially to take part in the u-ridge of labial basin. The other crest ~~goes~~ lingually ~~to mesially~~ close the lingual basin.

~~The row~~ *BB* includes three cusps in MNHN.F.SNP 2 Ma. In MNHN.F.SNP 335 W, the cusps cannot be described because of the wear. ~~The cusp~~ *BB1* is sub-equal in size ~~with~~ cusp *B4* and is situated at the same level. ~~The cusp~~ *BB1* is placed right next to cusps *B2* and *B3*, slightly more mesial than *B2-B3* notch. ~~The cusp~~ *BB2* is mesial to cusp *BB1* but slightly more lingual. This cusp is smaller and situated lower than cusp *BB1*. ~~The cusp~~ *BB3* is the ~~most mesial~~ of the tooth. This cusp is mesiodistally aligned with cusp *BB1*. A crest extends ~~the~~ row *BB* and ~~goes~~ labially to mesially close the lingual basin.

Comments on MNHN.F.SNP 14 FW. Only the distal part of MNHN.F.SNP 14 FW is preserved, with cusps *A1*, *B1*, *B2*, *BB1*, and a part of cusps *A2* and *B3*. Since morphometry is not

applicable, this specimen is referred to *Theroteinus rosieriensis* following the position of cusp *B2* in relation to cusps *B3* and *BB1*. MNHN.F.SNP 14 FW differs from other teeth described above by a less developed cusp *A1* and more developed cusp *B3*.

Wear.

Lower molariforms. In RBINS.RAS 62 FW, ~~all cusps are abraded by wear. In~~ MNHN.F.SNP 309 W, RBINS.RAS 74 FW, and RBINS.RAS 77 FW, all cusps are abraded by wear. The labial side of row *b* shows a large, concave surface of wear which extends from the distal extremity of cusp *b2* to cusp *b4*. It is difficult to say if this concavity was present before wear or not, but it shows traces of wear, like the sides of basin. MNHN.F.SNP 487 W also shows ~~a~~ wear ~~of~~ the entire surface of the tooth but several facets are present. ~~The cusp~~ *a1* shows a steep, distolabial facet. ~~The cusp~~ *a2* shows a steep, distal facet on its apex connected with a steep, distolingual facet on its lingual side. ~~The cusp~~ *b1* shows a horizontal facet. ~~The cusp~~ *b2* is partially truncated by a concave, shallow, labio-distolabial facet, which extends on cusp *b4*. The apex of cusp *b4* shows a horizontal, distal facet.

Upper molariforms. In MNHN.F.SNP 2 Ma, only the apices of cusps are abraded by wear. In MNHN.F.SNP 335 W, the cusps are more abraded and show several facets. ~~The cusp~~ *A1* shows a steep, distal facet. ~~The cusp~~ *A3* ~~seems to show~~ a steep, mesial facet. ~~The cusp~~ *B2* shows a shallow, mesiolabial facet. Other cusps of row *B* show one steep, mesial facet. ~~The row~~ *BB* shows one steep, mesial facet. In MNHN.F.SNP 14 FW, the wear ~~seems to be~~ more important. ~~The cusp~~ *A1* shows a shallow, distal facet~~. The~~ cusp *A2* ~~shows~~ a large, horizontal, labial facet. The cusp *B1* shows a horizontal distal facet. The cusp *B2* shows a horizontal facet. ~~The cusp~~ *B3* ~~seems to show~~ a shallow, mesial facet but is partially broken. ~~The cusp~~ BB1 shows a shallow, mesiolabial facet.

Reconstruction of the dental row of *Theroteinus*. In a so poorly-known group such as Haramiyida, the reconstruction of the dental rows from isolated teeth is notoriously difficult. Although five genera with complete or partial dentitions have been discovered in the last twenty years (Jenkins et al., 1997; Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014), there is no comparative study to provide elements on inter-specific and ontogenetic variations. The

reconstruction of the dental row of *Theroteinus* is complicated by two additional problems: (i) the small number of specimens (n=20) which prevents to evaluate the intra-specific variations, and (ii) the absence of premolariform specimens.

In upper molarifoms, the variations of development of cusps *A1* and *B1* and of the number of elements on the distolingual side of cusp *B2* can be related to the tooth position but also to individual or ontogenetic variations.

~~In lower molariforms, three specimens~~ show characters possibly related to tooth position. MNHN.F.SNP 61 W ~~shows a~~ cusp *b2* more distal in comparison with cusp a1 than other specimens. The first molar of *Haramiyavia* Jenkins, Gatesy, Shubin & Amaral, 1997 shows a similar character which may be a clue for a more mesial position in the dental row. MNHN.F.SNP 487 W ~~shows a~~ row *b* less high than in other specimens, cusp *b2* is especially much smaller in comparison with cusp *a1*. This difference of height is present in premolariforms of some haramiyids such as *Thomasia* as well, and it may consequently be a clue for a more mesial position in the dental row. However, MNHN.F.SNP 487 W does not show the distal shift of cusp *b2* seen in MNHN.F.SNP 61 W and the difference of height may also be related to ontogenetic variation~~s~~. MNHN.F.SNP 497 W shows a distally reduced row *b*, especially cusp *b4*. Since this specimen does not show characters of the other two specimens, this reduction of row *b* may be a clue for the last locus in the dental row. Indeed, this locus displays often a partial reduction of the crown in other groups of mammaliaforms (*e.g.*, Debuysschere, 2016). Since the reduction of row *b* could modify the occlusal function of the tooth, this interpretation may imply either that the last upper locus displays an equivalent reduction, or that this part of the tooth does not occlude with opposite teeth (*i.e.*, a more mesial position of the last upper locus).

Comparisons

Identification of *Theroteinus* species

The reappraisal of *Theroteinus nikolai* and the erection of *Theroteinus rosieriensis* sp. nov. are based on morphometric and morphologic characters.

Morphometry. Measurements of the *Theroteinus* material are presented in Table 1 and descriptive statistics in Table 2. Because of the small number of upper molariforms (n=4), no

583 statistical test can be made to support this discussion. Statistical tests are possible on lower
584 molariforms, but ~~their interpretation needs to be cautious~~ because ~~specimens are few numerous~~
585 (n=12). Means have been compared by the Welch's *t*-test, which is a variant of the Student's *t*-
586 test (command 't.test()' in R software). This test assumes that data are normally distributed. This
587 hypothesis has been tested by the Shapiro-Wilk test (command 'shapiro.test()' in R software),
588 without rejection of the null hypothesis (Table S2). The results of the *t*-test are presented in
589 Table 3. Graphically, the figure 7A shows two sets of upper teeth which do not overlap either by
590 length or by width, and two sets of lower teeth which slightly overlap. ~~The figure~~ 7B shows that
591 the same sets are present in length/width ratio, but with a more important overlapping between
592 sets of lower teeth. Since differences of means in length, width, and length/width ratio are
593 statistically significant (Table 3), specimens are divided between elongated small teeth and
594 stocky large teeth.
595 **Morphology.** In upper molariforms, two sets can be defined by the position of cusp *B2* which is
596 either mesiodistally aligned with cusps *B3* and *B4*, or lingually shifted to face the lingual basin.
597 In lower molariforms, two sets can be defined by the position of cusp *b4* which is either aligned
598 with row *b*, or lingually shifted to face the saddle. Both of these variations are related ~~by~~ the
599 occlusal pattern. Indeed, cusp B2 occludes lingually to cusp b4, consequently the latter cannot be
600 shifted lingually if the former is not shifted as well. ~~The table~~ 4 presents other morphological
601 differences between sets defined above. However, in the current stage of knowledge, it is
602 difficult to say if these differences are related to taxonomic, ontogenetic or individual variations.
603 The sets defined by morphologic and morphometric characters perfectly match. The lower and
604 upper molariforms are associated following characters presented above and the two sets are
605 considered as two species of genus *Theroteinus*. The set including MNHN.F.SNP 78 W (defined
606 as holotype by Sigogneau-Russell, Frank & Hemmerlé, 1986) is identified as *Theroteinus nikolai*
607 and the second set is identified as *Theroteinus rosieriensis* sp. nov. Since the new hypodigm of
608 *T. nikolai* includes all specimens referred to *Theroteinus* sp. described by Hahn, Sigogneau-
609 Russell & Wouters (1989), ~~*Theroteinus* sp. is a subjective synonym of~~ *Theroteinus nikolai*.
610
611 **Comparisons with other haramiyids**
612

Theroteinus differs from all other known haramiyids by low and massive cusps, separated by very shallow notches and by short and narrow basins in comparison with the size of the tooth. This genus differs also by a small number of cusps in each row, especially only two cusps in row *a* (character seen only in some specimens of *Thomasia*).

Theroteinus possibly shares the presence of a supplementary upper lingual row *BB* with *Eleutherodon* Kermack, Kermack, Lees & Mills, 1998 (Middle Jurassic, England), *Megaconus* Zhou, Wu, Martin & Luo, 2013 (Middle Jurassic, China), and *Millsodon* Butler & Hooker, 2005 (Middle Jurassic, England). However, recognizing this similarity depends on the different interpretations of the specimens concerned, especially on the orientation of the teeth.

Following the orientation of upper molariforms of *Eleutherodon* proposed by Kermack et al. (1998), Butler (2000) named the labial row *A*, the middle row *B*, and the lingual row *BB*, which corresponds to the pattern of *Theroteinus*. However, Meng et al. (2014: p. 29) proposed a second interpretation based on the comparison of the wear pattern of *Eleutherodon* with the wear pattern of *Arboroharamiya* Zheng, Bi, Wang & Meng, 2013. In this second interpretation, the labiolingual axis is inverted (Meng et al., 2014: Fig. 13). Although Meng et al. (2014) did not explicitly explain how they named the rows, it seems that they considered row *A* of Butler (2000) as row *B*, row *B* as row *A* and row *BB* as supplementary elements on the labial side of the tooth. As consequence, if we accept the interpretation of Meng et al. (2014), as the author does, *Eleutherodon* does not share the presence of row *BB* with *Theroteinus*.

Zhou et al. (2013) did not name the rows of cusps of upper teeth of *Megaconus*. However, since the ultimate tooth shows only two rows, it is more parsimonious to consider these rows as rows *A* and *B*, which implies that the third lingual row present in the two previous teeth would be a row *BB*. This interpretation is consistent with the few published comments on occlusion of *Megaconus* such as that of Zhou et al. (2013: Supplementary Information: p. 6): “[l]ower molars have two multicusp rows that alternately occlude in the two valleys between the three rows of cusps of M1 and M2”. However, Meng et al. (2014) questioned the orientation of the upper dentition of *Megaconus*. They proposed a reversal of the labiolingual axis and seemed to consider the labial row as a row *AA* (Meng et al., 2014: fig. 14). It is difficult to decide between both interpretations upon the available data. It must be emphasized that both orientations are given with few details on the definition of rows and on the relationships between them, which

643 authorizes several interpretations and prevents to conclude on presence of row *BB* in *Megaconus*
644 molariforms.
645 The comparison with *Millsodon* is based on a specimen BDUC J 3, which is considered as a
646 probable upper molar by Butler & Hooker (2005: p. 192). If this interpretation is accepted, this
647 specimen shows ~~a~~ row *BB* as *Theroteinus*, but it differs strongly from the latter by relationships
648 of size and position between other cusps. Indeed, the pattern of cusps is very peculiar for an
649 upper molariform and the two published interpretations of the specimen are very different from
650 each other (Butler & Hooker, 2005 *contra* Hahn & Hahn, 2006) (Fig. 8A-B). The sole argument
651 supporting the interpretation of BDUC J 3 as an upper molariform is the presence of a third
652 cusps row. The rest of the crown looks more like a lower molariform, and can be described as
653 follows: (i) a first row of cusps including a cusp much larger than others, (ii) a second row of
654 cusps, which are similar in size with small cusps of the first row, (iii) in the second row the
655 largest cusp is close to the large cusp of the first row but not labiolingually aligned with it, and
656 (iv) a cusp located at one extremity of the tooth, aligned with the second row, but separated from
657 it by the large cusp. No one other haramiyid upper tooth matches this pattern, unlike lower
658 molariforms of *Thomasia* and *Haramiyavia*. This new interpretation of ~~the~~ specimen BDUC J 3
659 as a lower molariform (Fig. 8C) is favoured here and implies two consequences. First, the
660 referral of ~~the~~ specimen BDUC J 3 to genus *Millsodon* needs a reassessment. Second, the
661 specimen can be compared with lower molariforms of *Theroteinus*. Several characters are shared
662 by these teeth: (i) the presence of few cusps by row, (ii) low and obtuse cusps, (iii) and a short
663 and narrow basin. Moreover, the third row of BDUC J 3, which is labial in this interpretation,
664 can be considered as development of the labial bulge present in some specimens of *Theroteinus*
665 (Figs. 4B-C, 5). However, new examination of BDUC J 3 would be necessary to discuss further
666 these points, which is impossible as this specimen is ~~said to be~~ lost ~~by~~ Butler & Hooker (2005: p
667 191).
668
669 **Discussion**
670
671 *Theroteinus* is referred to Haramiyida because of the presence of parallel rows of cusps.
672 Moreover, its molariforms show a pattern of cusps in size and relative position which is strongly
673 similar to patterns seen in *Thomasia* and *Haramiyavia*. In addition, the occlusal pattern of

Theroteinus is similar to the pattern of *Thomasia* with row *B* occluding ~~in~~ the lower basin. However, *Theroteinus* is very peculiar among haramiyids. The genus is defined by characteristic morphological characters (see above) and by a different masticatory movement. Indeed, *Theroteinus* is the only ~~one~~ haramiyid for which the wear pattern does not highlight a horizontal movement of the jaw during mastication (Sigogneau-Russell, Frank & Hemmerlé, 1986 and see above). Such a wear pattern and the small size of the basins support an essentially vertical masticatory movement. Because of these differences, *Theroteinus* has occupied since a long time a special place in the systematics of haramiyids, either as sister-group of the whole order Haramiyida (Hahn, Sigogneau-Russell & Wouters, 1989) or isolated in a sub-order (Butler, 2000; Hahn & Hahn, 2006). In the absence of a relevant cladistic analysis including *Theroteinus*, the sub-order Theroteinida is conservatively used in order not to complicate the taxonomy of haramiyids, which has already ~~known~~ many changes. In the same purpose, the name 'Theroteinida' is used unchanged although it would be best to change it. As underlined by Hahn & Hahn (2006: p. 189), the suffix of the name of a sub-order should be different from the suffix of the name of the including order. However, the suffix '-ina' suggested by Hahn & Hahn (2006: p. 189) cannot be used since it is reserved for the name of a subtribe by ~~the~~ article 29.2 of the ICZN (International Commission on Zoological Nomenclature, 2000).

The only ~~one~~ ~~taxa~~ closely related to *Theroteinus* is *Millsodon*, which is considered as a Theroteinidae by Hahn & Hahn (2006). Butler & Hooker (2005: p. 192) compared the upper tooth of *Millsodon* with the upper molariforms of *Theroteinus* and suggested that *Millsodon* could be “a derivative of the Theroteinidae or a specialised relative of the Haramiyidae”. However, Butler & Hooker (2005) considered *Millsodon* as indeterminate at familial rank and did not compare its lower molariforms with lower molariforms of *Theroteinus*. Hahn & Hahn (2006) considered that lower molariforms of *Millsodon* can be derived from lower molariforms of *Theroteinus*. This interpretation is based on specimen MNHN.F.SNP 226 W. Hahn & Hahn (2006: p. 184) considered that differences between this specimen and other lower molariforms of *Theroteinus* cannot be explained only by wear and that this specimen represents “a new taxonomical unit (perhaps a genus and a species)” and ~~an~~ intermediate between *Theroteinus* and *Millsodon*. This interpretation is questionable. First, the specimen MNHN.F.SNP 226 W is very poorly preserved, not only because of wear during life but also probably because of taphonomical processes. ~~Submitting~~ a new genus and an evolutionary scenario only on the base

of such a specimen ~~difficult to describe is highly hazardous~~. Second, comparisons between *Theroteinus* and *Millsodon* meet difficulties. On the one hand, the description of the upper tooth of *Millsodon* is questionable (see above). On the other hand, all lower teeth of *Millsodon* are heavily worn (e.g., Butler & Hooker, 2005: Fig.1.D-E), and the cusps are difficult to ~~describe~~. However, all specimens of *Millsodon* clearly show a well-developed basin, which is distinctive from *Theroteinus*. Consequently, the family Theroteinidae is considered here as monogeneric.

Acknowledgments

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804

Figure 1(on next page)

Views of CT-scan reconstructions of *Theroteinus nikolai* molariforms.

A, MNHN.F.SNP 78 W, right upper, holotype; **B**, MNHN.F.SNP 722, right upper; **C**, MNHN.F.SNP 226 W, left lower. 1, occlusal view; 2, distal view; 3, labial view; 4, mesial view; 5, lingual view. 'me' indicates mesial extremity and 'li' indicates lingual side.

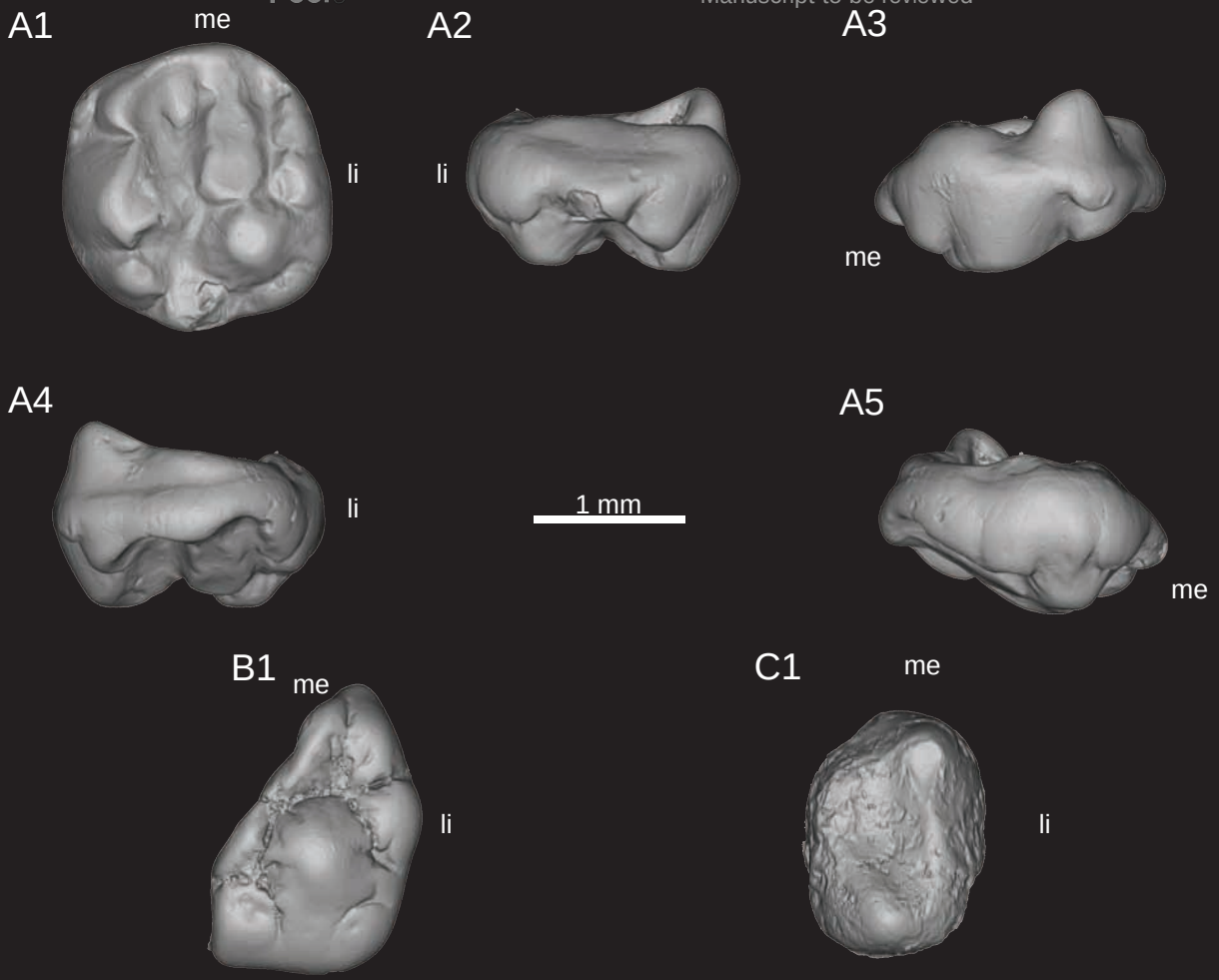

A1
me
li
A2
li
A3
me
A4
li
1 mm
A5
me
B1
me
li
C1
me
li

Figure 2(on next page)

Views of CT-scan reconstructions of *Theroteinus nikolai* lower molariforms.

A, MNHN.F.SNP 61 W, right; **B**, MNHN.F.SNP 366 W, right; **C**, MNHN.F.SNP 497 W, right. 1, occlusal view; 2, distal view; 3, labial view; 4, mesial view; 5, lingual view. 'me' indicates mesial extremity and 'li' indicates lingual side.

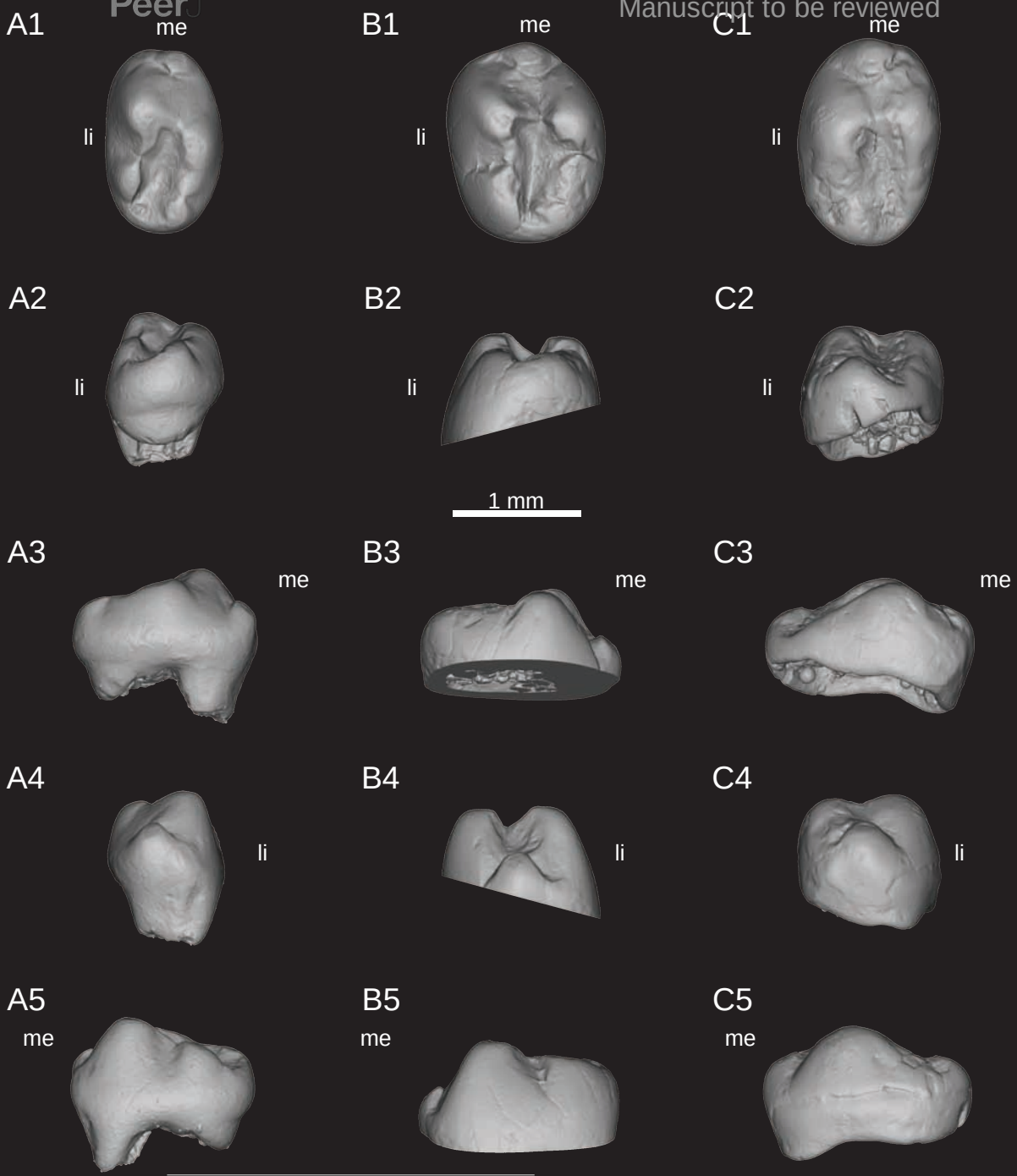


Figure 3(on next page)

Sketch drawings of *Theroteinus nikolai* molariforms in occlusal views.

A, MNHN.F.SNP 78 W, right upper, holotype; **B**, MNHN.F.SNP 61 W, right lower; **C**, MNHN.F.SNP 366 W, right lower; **D**, MNHN.F.SNP 497 W, right lower; **E**, MNHN.F.SNP 787, right lower. Right-angled arrow indicates mesial extremity and lingual side. Letters in italics correspond to cusp nomenclature.

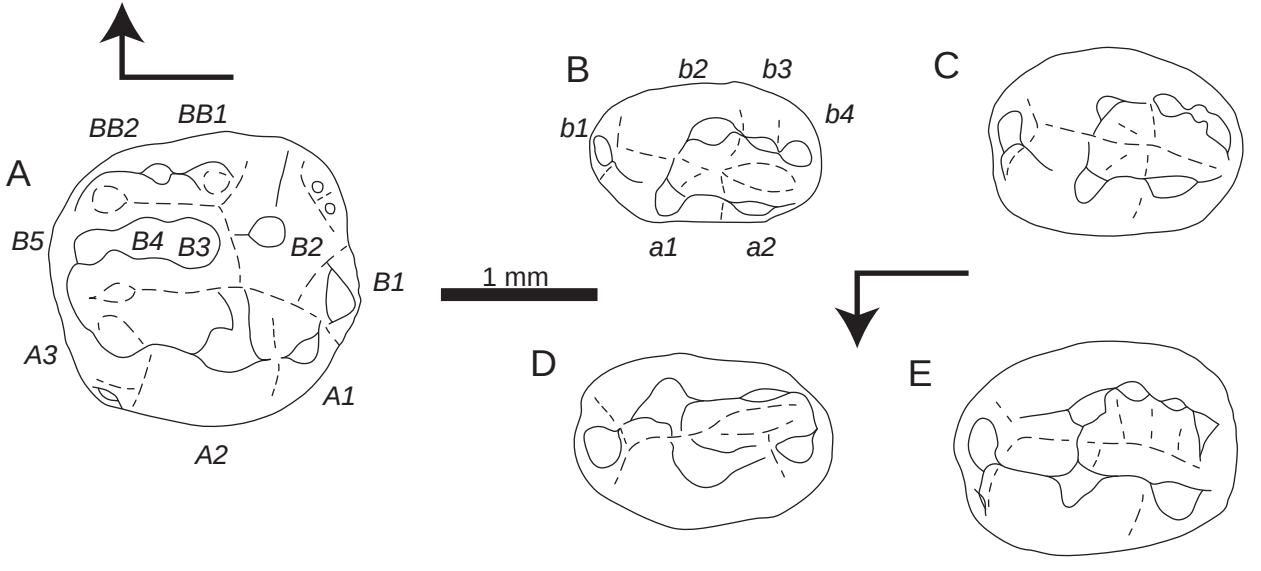

A
BB2
BB1
B5
B4
B3
B2
B1
A3
A1
A2
B
b2
b3
b1
b4
a1
a2
1 mm
C
D
E

Figure 4(on next page)

Views of CT-scan reconstructions of *Theroteinus rosieriensis* molariforms.

A, MNHN.F.SNP 2 Ma, right upper, holotype; **B**, MNHN.F.SNP 309 W, left lower; **C**, MNHN.F.SNP 487 W, left lower. 1, occlusal view; 2, distal view; 3, labial view; 4, mesial view; 5, lingual view. 'me' indicates mesial extremity and 'li' indicates lingual side.

Figure 5(on next page)

SEM photographs of *Theroteinus rosieriensis* lower molariforms.

A, RBINS.RAS 62 FW, right; **B**, RBINS.RAS 74 FW, right; **C**, RBINS.RAS 77 FW, right. 1, occlusal view; 2, distal view; 3, labial view; 4, mesial view; 5, lingual view. 'me' indicates mesial extremity and 'li' indicates lingual side.

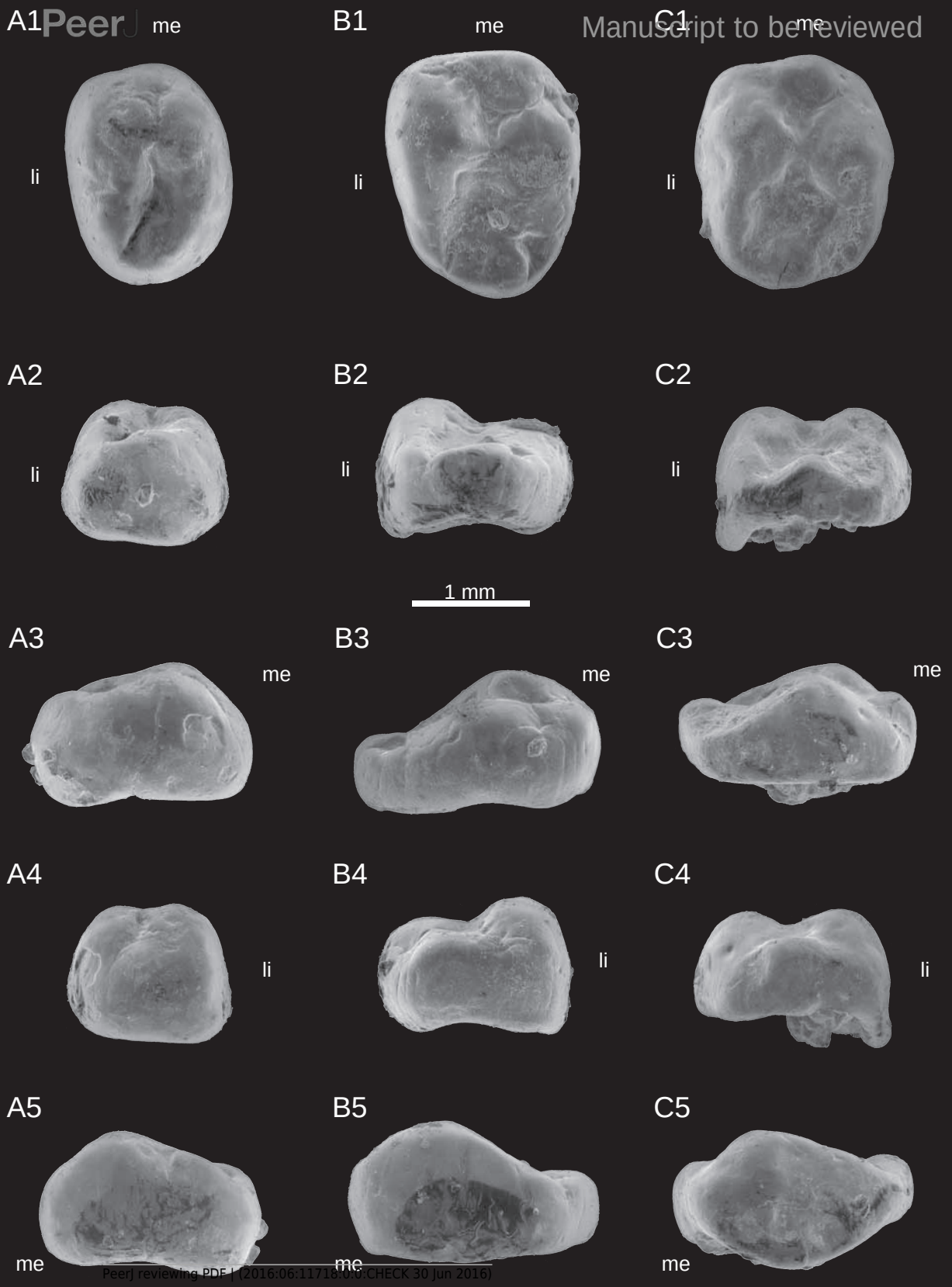
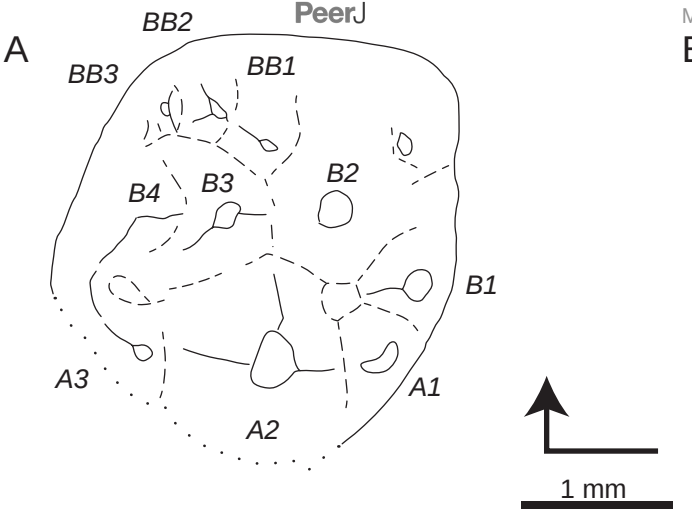
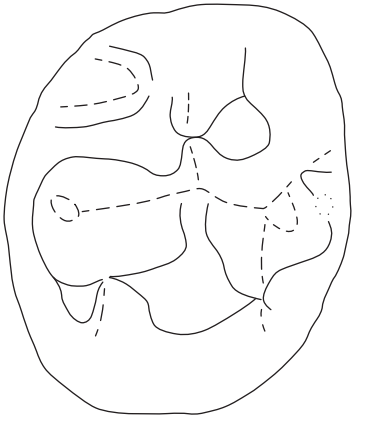


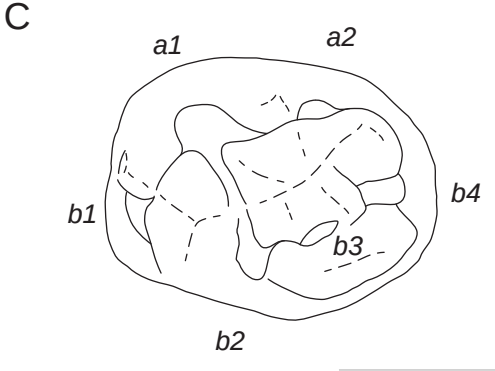
Figure 6(on next page)

Sketch drawings of *Theroteinus rosieriensis* molariforms in occlusal views.

A, MNHN.F.SNP 2 Ma, right upper, holotype; **B**, MNHN.F.SNP 335 W, right upper; **C**, MNHN.F.SNP 309 W, left lower; **D**, MNHN.F.SNP 487 W, left lower. Right-angled arrow indicates mesial extremity and lingual side. Letters in italics correspond to cusp nomenclature.


A
BB2
BB3
BB1
B4
B3
B2
B1
A3
A1
A2
1 mm


B


C
a1
a2
b1
b4
b3
b2

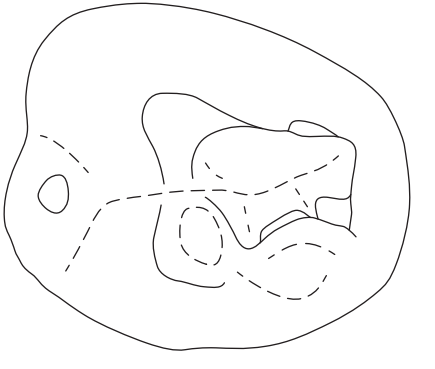

D

Figure 7 (on next page)

Scatterplots of Theroteinus specimens from Saint-Nicolas-de-Port according to (A) length w width (in mm) and (B) length/width ratio (measurements in Table 1).

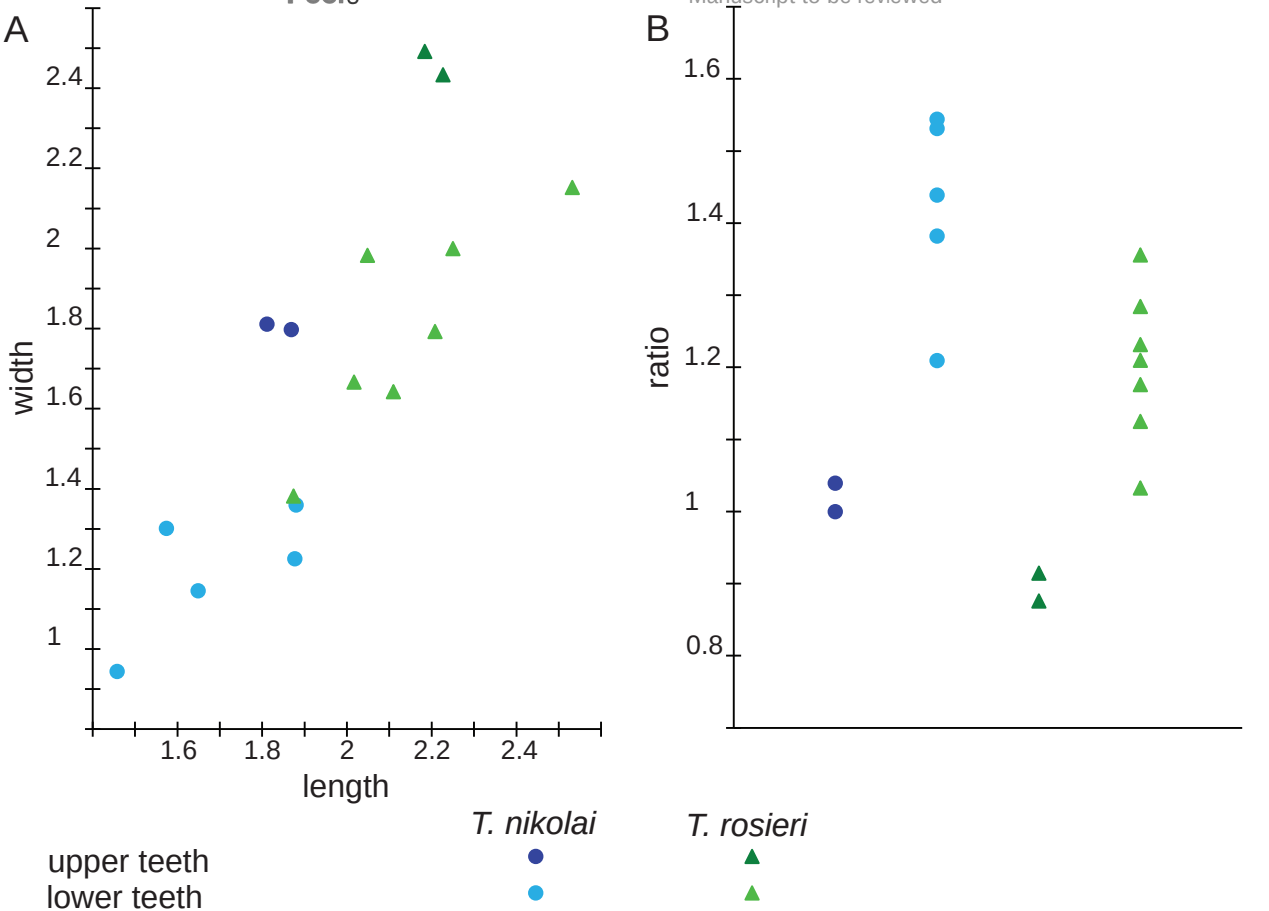

A
B
width
length
ratio
1
1.2
1.4
1.6
1.8
2
2.2
2.4
0.8
T. nikolai
T. rosieri
upper teeth
lower teeth

Figure 8(on next page)

Sketch drawings of specimen BDUC J 3 referred to *Millsodon* (Middle Jurassic, England), after Butler & Hooker (2005: Fig. 3C).

(**A**) interpretation of Butler & Hooker (2005); (**B**) interpretation of Hahn & Hahn (2006); (**C**) interpretation proposed here. Right-angled arrow indicates mesial extremity and lingual side. Letters in italics correspond to cusp nomenclature.

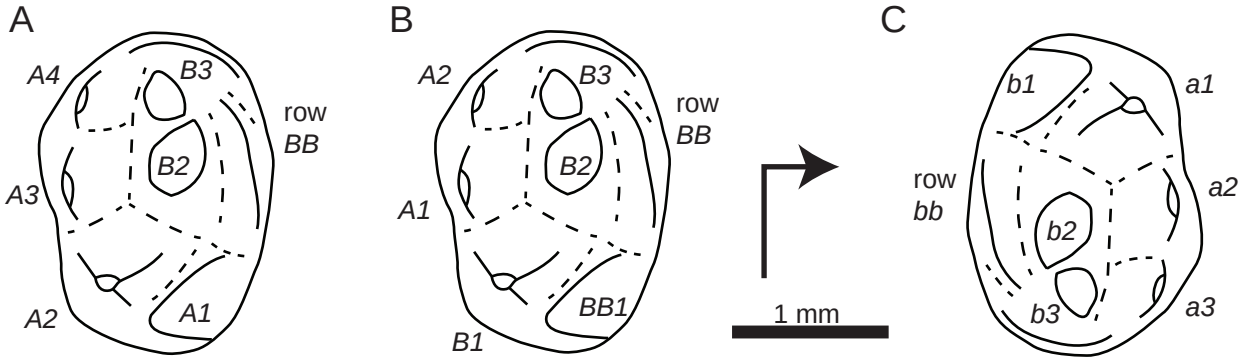

A
A4
B3
row
BB
B2
A3
A2
A1
B
A2
B3
row
BB
B2
A1
BB1
B1
1 mm
C
b1
a1
row
bb
a2
b2
b3
a3

Table 1(on next page)

Dental measurements (in mm) of *Theroteinus* molarifoms from Saint-Nicolas-de-Port (Upper Triassic, France).

L: mesiodistal length, W: labiolingual width, R: length/width ratio.

1

Material	L (mm)	W (mm)	R	Material	L (mm)	W (mm)	R
Theroteinus nikolai							
Upper teeth							
MNHN.F.SNP 78 W	1.87	1.8	1.04	RBINS.RAS 103 FW	1.81	1.81	1.00
Lower teeth							
MNHN.F.SNP 61 W	1.46	0.94	1.54	MNH.F.SNP 226 W	1.88	1.23	1.53
MNHN.F.SNP 366 W	1.57	1.3	1.21	MNHN.F.SNP 497 W	1.65	1.15	1.44
MNHN.F.SNP 787	1.88	1.36	1.38				
Theroteinus rosieri							
Upper teeth							
MNHN.SNP 2 Ma	2,41			MNHN.SNP 335 W	2.18	2.49	0.88
RBINS.RAS 801	2.23	2.43	0.91				
Lower teeth							
MNHN.SNP 309 W	2.05	1.98	1.03	MNHN.F.SNP 487 W	2.53	2.15	1.18
RBINS.RAS 3 FW		1.92		RBINS.RAS 11 FW	2.21	1.79	1.23
RBINS.RAS 62 FW	1.87	1.38	1.36	RBINS.RAS 74 FW	2.11	1.64	1.28
RBINS.RAS 77 FW	2.02	1.67	1.21	RBINS.RAS 800	2.25	2.00	1.13

2

3

Table 2(on next page)

Means, standard deviations and medians for length, width (in mm), and length/width ratio for molariforms of *Theroteinus* from Saint-Nicolas-de-Port (Upper Triassic, France).

1

Taxa	Series	Measurements	Means	Standard Deviations	Medians
T. nikolai	upper	length (mm)	1.8401	0.0407	1.8401
		width (mm)	1.8045	0.0097	1.8045
		length/widht	1.0198	0.028	1.0198
	lower	length (mm)	1.6872	0.1871	1.6484
		width (mm)	1.1953	0.1619	1.2256
		length/widht	1.4211	0.136	1.4389
T. rosieriensis	upper	length (mm)	2.2736	0.1211	2.2264
		width (mm)	2.4628	0.0407	2.4628
		length/widht	0.8955	0.0272	0.8955
	lower	length (mm)	2.1482	0.2101	2.1098
		width (mm)	1.8179	0.2472	1.8585
		length/widht	1.2023	0.1054	1.2098

2

Table 3(on next page)

Statistical comparisons of the means of lower molariforms of *Theroteinus nikolai* and *Theroteinus rosieriensis* from Saint-Nicolas-de-Port (Upper Triassic, France) by t-test.

Normality of the data has been tested by Shapiro-Wilk Test (Table S2), the alternative hypothesis is “true difference in means is not equal to 0”, * indicates statistically significant results (threshold = 0.05).

1

Measurements tested	Value of the test (t)	95% confidence interval	p-value
length	-3.9959	-0.7204336;-0.2016236	0.002882*
width	-5.4858	-0.8726922;-0.3725728	0.0001959*
length/width	3.0109	0.04829294;0.38939849	0.01875*

2

Table 4(on next page)

Summary of differences between lower and upper molariforms of *Theroteinus nikolai* and *Theroteinus rosieriensis* which are not included in diagnoses.

1

	T. nikolai	*T. rosieriensis*
lower teeth	- a vertical, weak medial ridge in the middle of the labial side of cusp *a2* - alignment of the long axes of cusps *b3* and *b4* - a lingual carina on cusp *b4*	- a very high saddle - cusp *a2* twice times smaller than cusp *a1* - sub-equality of the slopes of lingual and labial sides of cusp *a2* - a mesiodistally less extended base of cusp *b2* - cusp *b3* much smaller than cusp *b1* - cusp *b3* slightly lingual to cusp *b2*
upper teeth	- mesiodistal alignement of thrre cusps *A* - a small cusp under the labial side of cusp *A3* - a distally curved semi-circular cusp *B1*	- cusp *A1* slightly longer than cusp *A3* - a concave surface on the mesiolingual side of cusp *A2* - four cusps in row *B* - cusp *B1* mesiodisally aligned with the saddle - cusp *B3* more labial than cusp *B2* - three cusp in row *BB* - cusp *BB1* slightly more mesial than *B2-B3* notch

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